ZooKeys 514: 73–91 (2015)
doi: 10.3897/zookeys.514.10013
http://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A new species of nectar-feeding bat, genus *Lonchophylla*, from the Caatinga of Brazil (Chiroptera, Phyllostomidae)

Ricardo Moratelli[1,2], Daniela Dias[3]

1 *Fiocruz Mata Atlântica, Fundação Oswaldo Cruz, CEP 22713-375, Rio de Janeiro, Brazil* **2** *Division of Mammals, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013-7012, U.S.A.* **3** *Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz, CEP 21040-900, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil*

Corresponding author: *Ricardo Moratelli* (rmoratelli@fiocruz.br)

Academic editor: *W. Bogdanowicz* | Received 19 May 2014 | Accepted 3 July 2015 | Published 22 July 2015

http://zoobank.org/3E05B89A-307B-4792-B85A-D7FEB949F829

Citation: Moratelli R, Dias D (2015) A new species of nectar-feeding bat, genus *Lonchophylla*, from the Caatinga of Brazil (Chiroptera, Phyllostomidae). ZooKeys 514: 73–91. doi: 10.3897/zookeys.514.10013

Abstract

We describe *Lonchophylla inexpectata* **sp. n.** from the Caatinga of Brazil. This new species can be distinguished from all known species of *Lonchophylla* that occur in Brazil by dental traits, cranial size, and fur colour. Specimens of *L. inexpectata* have been misidentified as *L. mordax*; but *L. inexpectata* is a pale-venter species, similar in external appearance to *L. dekeyseri*. We have found *L. inexpectata* in the Caatinga of North-eastern Brazil; *L. mordax* along the eastern border of the Caatinga and in the Atlantic Forest–Caatinga ecotone in North-eastern Brazil; and *L. dekeyseri* in the Cerrado of Mid-western Brazil, in the Brazilian Cerrado–Caatinga ecotone, and as far west as the Cerrado of Bolivia.

Keywords

Atlantic Forest, Caatinga, Cerrado, *Lonchophylla inexpectata*, *Lonchophylla dekeyseri*, *Lonchophylla mordax*, North-eastern Brazil

Introduction

Lonchophylla Thomas, 1903 (Phyllostomidae) comprises 12 species of nectar-feeding bats restricted to the Neotropics (Griffiths and Gardner 2008, Parlos et al. 2014). Parlos et al. (2014) revised the Lonchophyllinae and established *Hsunycteris* as a new genus to include the smaller species formerly known as the *Lonchophylla thomasi* complex.

Copyright *Ricardo Moratelli, Daniela Dias*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

However, their revision did not include the Brazilian species *L. mordax* Thomas, 1903, *L. bokermanni* Sazima et al., 1978, *L. dekeyseri* Taddei et al., 1983, and *L. peracchii* Dias et al., 2013. During our assessment of these Brazilian species we found evidence of another new taxon based on specimens from the Brazilian Caatinga we found in museum collections. Some specimens of this previously undescribed species have been misidentified as *L. mordax* for more than a century.

Lonchophylla mordax was described from Lamarão, Bahia (Thomas 1903), with subsequent records ascribed to specimens from other localities in Northern ([N] Handley 1967, Piccinini 1974, Koopman 1981), North-eastern ([NE] Vieira 1955, Sazima et al. 1978, 1983, Mares et al. 1981, Willig 1983, Astúa and Guerra 2008), Mid-western ([MW] Peracchi et al. 2011), and South-eastern Brazil ([SE] Pereira-Barreto et al. 1968, Taddei et al. 1978, Pedro and Passos 1995, Esbérard et al. 2006, Dias et al. 2002, Esbérard 2003). Handley (1966) synonymized *L. concava* Goldman, 1914 under *L. mordax*, thus enlarging its geographic distribution westward into western Colombia and Ecuador, and northwestward into Costa Rica. This arrangement was rejected by Albuja and Gardner (2005), who recognized *L. concava* as a distinct species. Based on the records available, bat biologists have assumed that *L. mordax* was restricted to eastern South America, with records from the Amazon Forest of N Brazil, eastward to xeric habitats in NE Brazil, and southward to the Atlantic Forest of SE Brazil, including transitional areas between these last two biomes (see Griffiths and Gardner 2008, Peracchi et al. 2011).

Thomas's (1903) description of *L. mordax* is based on eight specimens from Lamarão, Bahia collected by Alphonse Robert in 1903. Lamarão is in the *agreste* sub region of NE Brazil, which is a narrow transition zone between the coastal Atlantic Forest to the east and the semiarid Caatinga on the west (Prado 2003). According to local residents, the vegetation in Lamarão and adjacent areas during the first half of the 20th century was dominated by tall forests, which is characteristic of the transitional vegetation between the Atlantic Forest and Caatinga. Throughout the last century, land-use practices have converted the region into a semi-arid environment that resembles caatinga habitats. The type material of *L. mordax*, originally deposited in the Natural History Museum, London (BM), includes the holotype (BM 1903.9.5.34) and seven paratypes. One of the paratypes was sent to the Smithsonian's National Museum of Natural History, Washington, DC (USNM 123392). A few years after Thomas described *L. mordax*, a series of *Lonchophylla* were collected in Barra, Bahia by Ernest Garbe and Robert H. Becker in 1908 and 1914, respectively. Barra, Bahia is in the *sertão* sub region (450 to 500 km west of Lamarão), a semi-arid environment that is characteristic of the Caatinga (Prado 2003). According to their labels, Garbe's and Becker's specimens from Barra were identified as *L. mordax* and either originally deposited or subsequently sent to museums in Brazil and United States of America. This material has been the basis for several subsequent published accounts on *L. mordax* (e.g., Lima 1926: 36, Vieira 1942: 321). As with the paratype of *L. mordax* (USNM 123392), one of those specimens collected by Garbe is housed in the Smithsonian's National Museum of Natural History (USNM 238008). After comparing skins and skulls of Garbe's and Thomas's USNM specimens from Barra (Caatinga, USNM 238008) and Lamarão (Atlantic Forest/Caatinga, USNM 123392),

we determined that the pale-venter *Lonchophylla* from Barra could be distinguished from *L. mordax*, and represented an undescribed species. Among distinctive traits distinguishing the Barra specimen from *L. mordax* are the paler colour of the ventral fur and the smaller skull that has a narrower and more delicate rostrum.

To test this hypothesis and further understand the geographic distribution of Brazilian species, we examined series of *Lonchophylla* from localities in the Caatinga, Cerrado, and Atlantic Forest, as well as from transitional zones between these habitats. The material used in our comparisons represents all *Lonchophylla* species known to occur in Brazil. During this process we found additional features that support our hypothesis that the pale-venter *Lonchophylla* from the Caatinga represents a new species, which we describe below.

Methods

The material we used in the comparisons includes series of *Lonchophylla* from the Caatinga of NE Brazil (Bahia [municipalities of Andaraí, Barra, Buíque], Ceará, Pernambuco, Piauí, Sergipe [Grota do Angico]); Cerrado of Bolivia (Santa Cruz) and Mid-western Brazil (Distrito Federal, Goiás, Mato Grosso do Sul); Atlantic Forest of SE Brazil (Espírito Santo, Rio de Janeiro); and the Atlantic Forest–Caatinga ecotone in NE Brazil (Bahia [Lamarão], Sergipe [Itabaiana]). This material includes representatives of all currently recognized Brazilian species of *Lonchophylla*, and includes primary and secondary types of *L. bokermanni* (6 specimens from the type series), *L. dekeyseri* (holotype and one paratype), *L. mordax* (holotype and one paratype), and *L. peracchii* (holotype and two paratypes). Vouchers are preserved in the American Museum of Natural History (AMNH, New York, USA); Carnegie Museum of Natural History (CM, Pittsburgh, USA); Museu Nacional (MN, Rio de Janeiro, Brazil); Muséum d'histoire naturelle (MHNG, Geneva, Switzerland); Natural History Museum (BM, London, England); Smithsonian's National Museum of Natural History (USNM, Washington DC, USA); Universidade Estadual Paulista Júlio de Mesquita Filho (DZSJRP, São José do Rio Preto, Brazil); Universidade Federal do Espírito Santo (UFES, Espírito Santo, Brazil); Universidade Federal Rural do Rio de Janeiro (ALP, LMD, Seropédica, Brazil). A complete list of specimens examined is in the Appendix. Most geographical coordinates follow Gardner's (2008) gazetteer of marginal localities.

Measurements in this report are from adults, and are either in millimetres (mm) or grams ([g] body mass). The body mass was recorded from skin labels. Other dimensions include: the forearm length (FA), from the elbow to the distal end of the forearm including carpals, measured with the wing partially folded; greatest length of skull (GLS), from the posteriormost point of the occiput to the tips of the upper inner incisors; condylo-incisive length (CIL), from the line connecting the occipital condyles to the tips of the upper inner incisors; basal length (BAL), from the anterior margin of the foramen magnum to the tips of the upper inner incisors; maxillary toothrow length (MTL), from the anterior surface of the upper canine, including the cingulum, to the posterior surface of M3; molariform toothrow length (M1M3), from the crown of M1 to

the crown of M3; breadth across canines (BAC), greatest breadth across outer surface of the crowns of upper canines, including cingulae; breadth across molars (BAM), greatest breadth across outer edges of the crowns of upper molars; postorbital breadth (POB), least breadth across frontals posterior to the postorbital bulges; braincase breadth (BCB), greatest breadth of the globular part of the braincase; mastoid breadth (MAB), greatest breadth across the mastoid region; mandibular length (MAL), from the mandibular symphysis to the condyloid process; and the mandibular toothrow length (MAN), from the anterior crown of the lower canine, including cingulum, to the posterior crown of m3. Craniodental measurements were taken under binocular dissection microscopes with low magnification (usually 6×). Dimensions were taken by only one of us, using digital callipers accurate to 0.02 mm. Measurements were recorded and analysed to the nearest 0.01 mm, but values were rounded off to 0.1 mm throughout the text because this is the smallest unit that allows accurate repeatability with callipers (Voss et al. 2013). Descriptive statistics (mean and range) were calculated for all dimensions. The statistical significance of differences among samples was assessed by single analyses of variance (one-way ANOVA). This statistics was performed in PAST (Hamer et al. 2001).

Discriminant Function Analysis (DFA) was used to compare taxa. For the analysis, we selected a subset of the cranial dimensions (GLS, CIL, MAB, BCB, POB, BAC, BAM, M1M3, MTL, MAL) to represent different axes of length and width of the skull. As multivariate procedures require complete datasets, missing values (< 3% of the total dataset) were substituted by means. Measurements were transformed to natural logarithms and the covariance matrices were computed considering all variables. DFA was performed in SPSS.

Nomenclature of tooth morphology follows Phillips (1971). Capitalized colour nomenclature follows Ridgway (1912).

Taxonomy

***Lonchophylla inexpectata* sp. n.**
http://zoobank.org/610DFBAE-1726-4666-9B3F-BDCC063D25D2
Figures 1, 2, 4, 5; Table 1

Lonchophylla mordax: Lima 1926: 76; not *Lonchophylla mordax* Thomas, 1903.
Lonchophylla mordax: Vieira 1942: 321; not *Lonchophylla mordax* Thomas, 1903.
Lonchophylla mordax: Taddei, Vizotto and Sazima 1983; not *Lonchophylla mordax* Thomas, 1903.
Lonchophylla dekeyseri: Woodman and Timm 2006: 450; part, not *Lonchophylla dekeyseri* Taddei, Vizotto & Sazima, 1983.
Lonchophylla mordax: Woodman and Timm 2006: 475; part, not *Lonchophylla mordax* Thomas, 1903.
Lonchophylla dekeyseri: Woodman 2007. Part, not *Lonchophylla dekeyseri* Taddei, Vizotto & Sazima, 1983.

Figure 1. Dorsal **A** and ventral **B** pelage of the holotype of *L. inexpectata* (USNM 238008). Scale bar: 10 mm.

Holotype. An adult male, USNM 238008, with skin and skull (Figures 1, 2), including mandible, collected by E. Garbe at Barra (12°42'S, 41°33'W), Bahia, Brazil, on January 1908. Skull and mandible are in good condition except for the minimally damaged anteriormost portion of the foramen magnum. The body is prepared as dry skin. Woodman and Timm (2006: 450) described USNM 238008 as a faded skin, but after comparison of its pelage colour with those from other specimens, only mem-

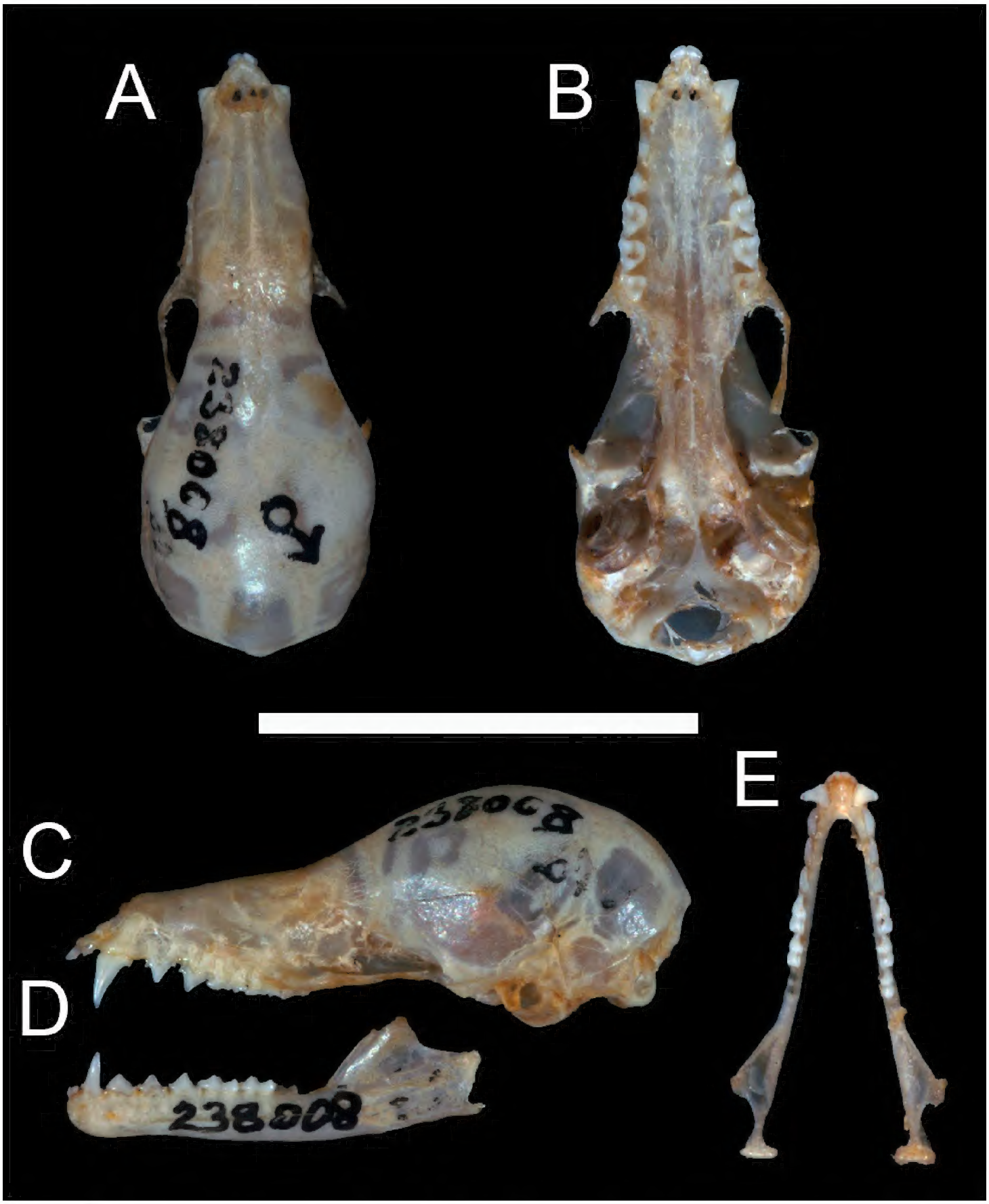

Figure 2. Dorsal **A**, ventral **B**, and lateral **C** views of the cranium, and lateral **D** and dorsal **E** views of the mandible of the holotype of *L. inexpectata* (USNM 238008). Scale bar: 15 mm.

branes seem to be faded. External and craniodental measurements for the holotype and paratypes are in Table 1.

Paratypes. The paratype series comprises 46 vouchers. Three paratypes are from the type locality in Barra, Bahia (AMNH 235608, FMNH 21077, 21078), and were collected by R. H. Becker in 1914. One is from Serra do Catimbau, Buíque, Pernambuco (FMNH 137414; 08°37'S, 37°09'W [coordinates for Catimbau National Park]),

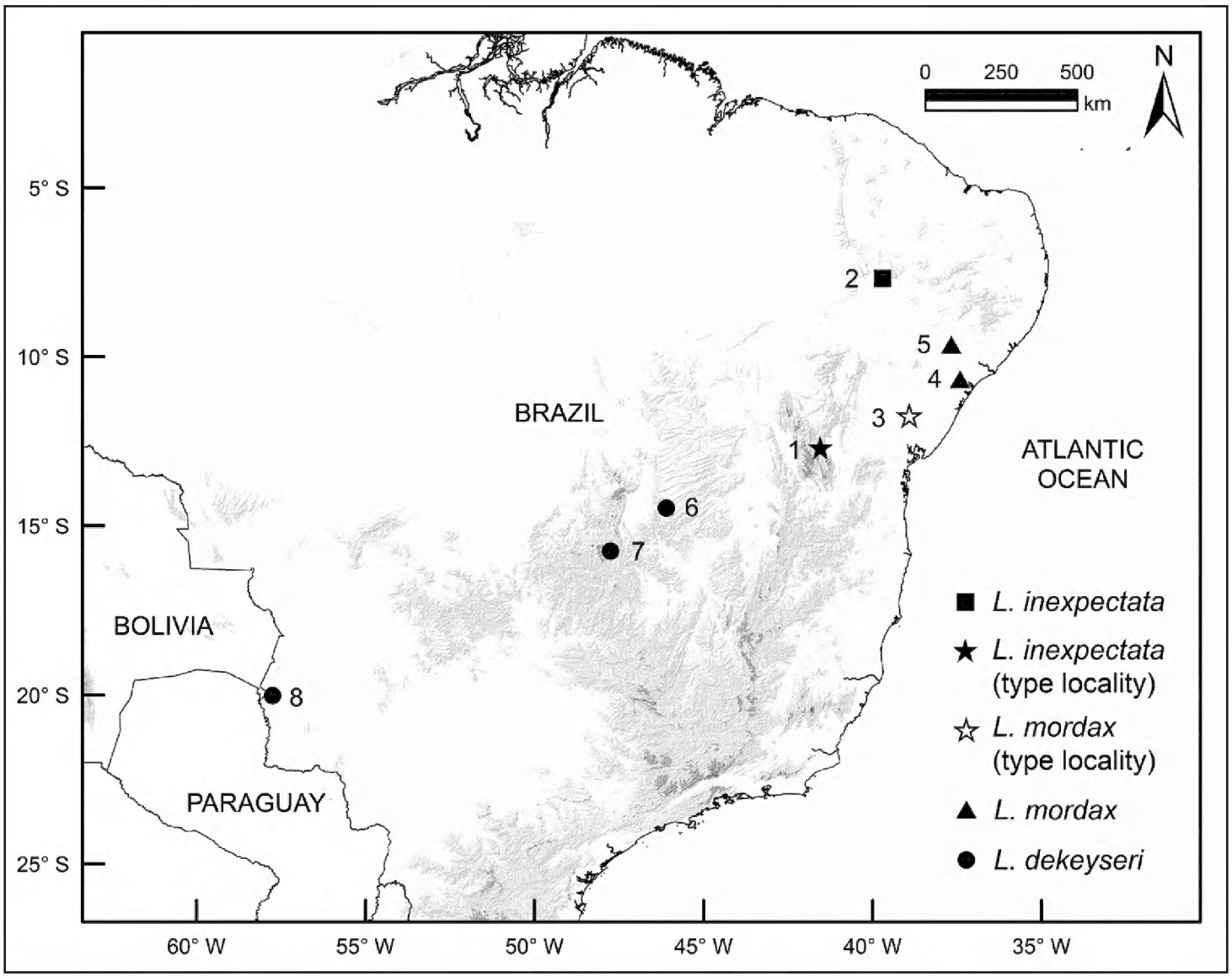

Figure 3. Map of part of South America showing the geographic distribution of samples we confirmed as *L. inexpectata* (black star [type locality] and square), *L. dekeyseri* (circles), and *L. mordax* (white star [type locality] and triangles). Localities 1, 2, 5 are in the Caatinga; localities 3, 4 are in the Caatinga–Atlantic Forest ecotone; and localities 6–8 are in the Cerrado.

and was collected by D. Guerra in 1970. Thirty-eight vouchers are from 17 km south of Exu, Pernambuco (CM 99413–99450; 07°41'S, 39°32'W), elevation ca. 480 m, and were collected by M. R. Willig in 1976. Paratypes from Barra (AMNH 235608, FMNH 21077, 21078), and Buíque (FMNH 137414) are in spirits, others are prepared as dry skin.

Other specimen. One additional specimen (ALP 3686) from the Caatinga of Andaraí, Bahia may represent *L. inexpectata*. The specimen is preserved in spirit, and the dentition is partially worn, preventing its unambiguous identification.

Distribution. *Lonchophylla inexpectata* occurs in the Caatinga of North-eastern (NE) Brazil, with confirmed records from Pernambuco (NE), and Bahia (NE) (Figure 3).

Diagnosis. *Lonchophylla inexpectata* can be distinguished from all South American species that occur east of the Andes by the following set of traits: presence of a lingual cusp in the P4, absence of a lingual cusp in the P3, absence of a deep longitudinal groove in the posterior face of the upper canine, proximal portion of the dorsal surface of the forearm not furred, and ventral fur pale.

Table 1. Body mass (g) and external and skull measurements (mm) of the holotype (USNM 238008) of *L. inexpectata*, and descriptive statistics for *L. inexpectata* (from Caatinga [type series]), *L. dekeyseri* (from Cerrado), and *L. mordax* (from Caatinga and Caatinga–Atlantic Forest ecotone).

	L. inexpectata	***L. inexpectata***	***L. dekeyseri***	***L. mordax***
	Holotype	**Mean**	**Mean**	**Mean**
	USNM 238008	(Min.–Max.) *N*	(Min.–Max.) *N*	(Min.–Max.) *N*
Body mass	–	**8.2**	–	–
		(7.0–9.5) *15*		
FA	**33.7**	**34.6**	**36.9**	**35.8**
		(32.3–36.4) *62*	(35.5–38.0) *15*	(34.5–37.4) *32*
GLS	**22.3**	**23.1**	**22.4*****	**23.6****
		(22.0–23.9) *38*	(22.0–22.7) *16*	(22.6–24.5) *24*
CIL	**20.8**	**21.7**	**21.0*****	**22.2*****
		(20.5–22.6) *37*	(20.4–21.4) *16*	(21.3–23.2) *24*
BAL	**19.1**	**19.8**	**19.1*****	**20.2****
		(18.7–20.7) *36*	(18.5–19.6) *16*	(19.6–20.8) *20*
MTL	**7.6**	**7.8**	**7.6****	**8.0*****
		(7.4–8.2) *45*	(7.3–7.9) *16*	(7.6–8.4) *26*
M1M3	–	**3.3**	**3.4***	**3.5*****
		(3.1–3.6) *40*	(3.3–3.6) *14*	(3.3–3.7) *30*
BAC	**3.4**	**3.6**	**3.7****	**3.7***
		(3.3–3.8) *44*	(3.4–3.9) *16*	(3.5–4.1) *27*
BAM	**4.8**	**5.1**	**5.1**	**5.3***
		(4.8–5.5) *43*	(4.9–5.3) *16*	(4.7–5.7) *26*
POB	**4.1**	**4.3**	**4.5*****	**4.3**
		(4.1–4.7) *46*	(4.2–4.6) *16*	(4.0–4.6) *27*
BCB	**7.9**	**8.3**	**8.4***	**8.5**
		(7.9–8.6) *46*	(8.0–8.7) *16*	(8.1–8.9) *27*
MAB	**8.5**	**9.0**	**9.1*****	**9.3***
		(8.5–9.6) *44*	(8.8–9.4) *16*	(8.9–9.7) *27*
MAL	**14.9**	**15.6**	**15.1*****	**16.1*****
		(14.1–16.3) *44*	(14.8–15.4) *16*	(15.5–17.0) *25*
MAN	**8.0**	**8.2**	**8.1***	**8.4*****
		(7.8–8.5) *43*	(7.7–8.4) *16*	(7.9–8.9) *25*

N = sample size (adults only, males and females combined). See "Methods" for variable abbreviations and Appendix for localities of specimens used in comparisons. One-way ANOVA for skull measurements is comparing *L. inexpectata* with *L. dekeyseri* and *L. mordax*: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Description and comparisons. Like other *Lonchophylla*, the dental formula of *L. inexpectata* is 2/2, 1/1, 2/3, 3/3 = 34. *Lonchophylla inexpectata*, *L. dekeyseri* and *L. bokermanni* are the three pale-venter Brazilian species of the genus, whereas *L. mordax* and *L. peracchii* have pale-brown ventral pelage. We did not find evidence of *L. bokermanni* and *L. peracchii* in sympatry with *L. inexpectata*—*L. bokermanni* is restricted to a small area in the Serra do Espinhaço, Cerrado of Minas Gerais; and

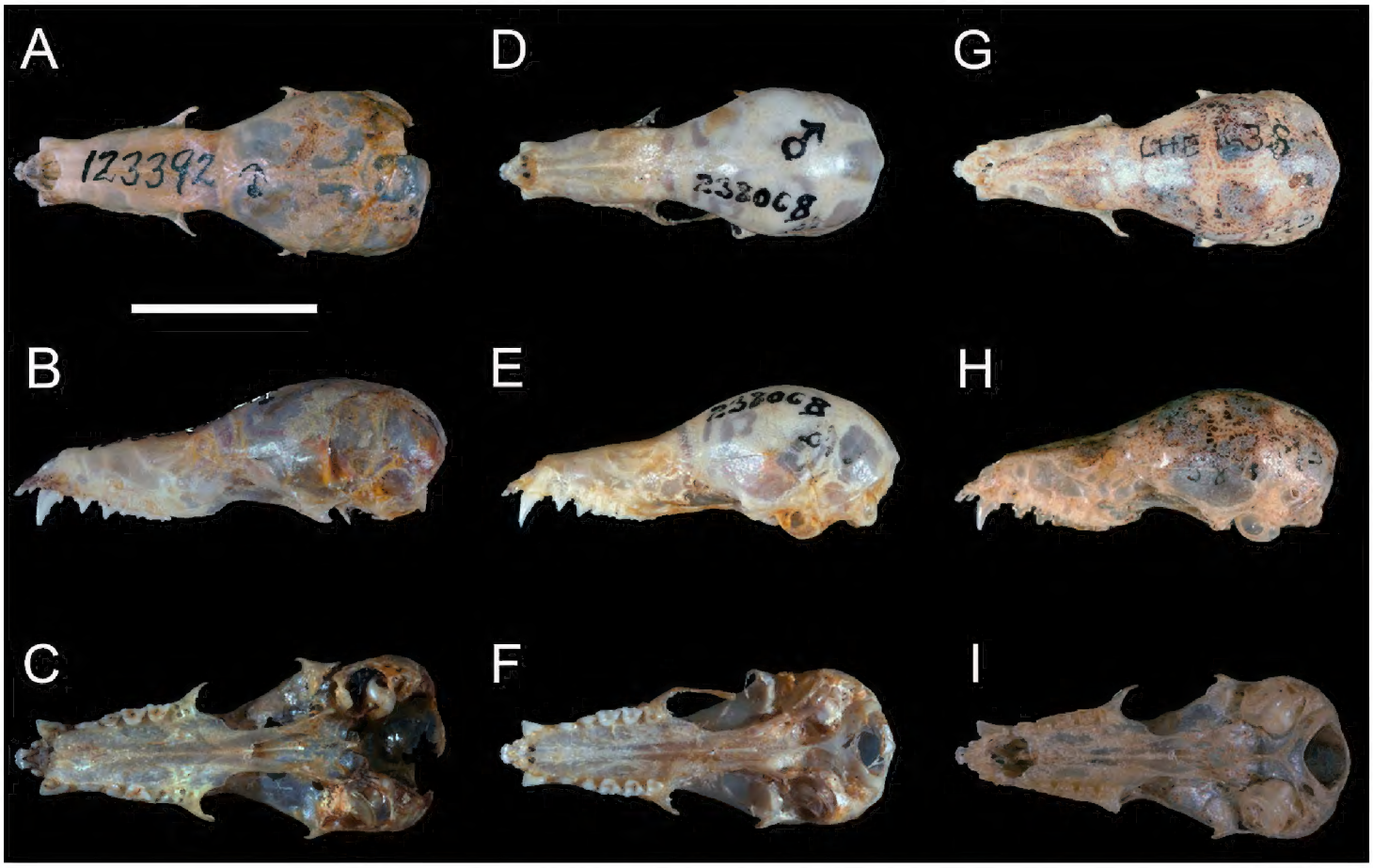

Figure 4. Dorsal (above), lateral (middle), and ventral (below) views of the skull of *L. mordax* (**A–C** [USNM 123392, paratype]), *L. inexpectata* (**D–F** [USNM 238008, holotype]), and *L. dekeyseri* (**G–I** [USNM 584472]). Scale bar: 10 mm.

L. peracchii occurs in the Atlantic Forest, from Espírito Santo southward to São Paulo. *Lonchophylla inexpectata* can be distinguished from these two species by the presence of a well-developed lingual cusp in the P4, with lingual root in the median portion of the tooth; absence of a groove along the anterior surface of the upper canines; and proximal portion of the dorsal surface of the forearm not covered with fur.

Based on the samples we have available, *L. inexpectata* resembles *L. dekeyseri* in the pale ventral fur, and *L. mordax* in the dental morphology. These three species overlap partially in external and cranial size, but in general, cranial measurements for *L. inexpectata* average significantly larger than those for *L. dekeyseri* and smaller than those for *L. mordax* (Table 1).

Lonchophylla mordax has been reported in the literature as a pale-venter species (e.g., Lima 1926, Vieira 1942, Taddei et al. 1983, Nogueira et al. 2007), and subsequent to the description of *L. dekeyseri*, these taxa have been considered the two pale-venter species from NE Brazil (see Taddei et al. 1983, Nogueira et al. 2007, Dias et al. 2013). However, after examining part of the type series of *L. mordax* (BM 1903.9.5.34 [holotype], USNM 123392 [paratype]), along with one other specimen from the same locality of the type series (MHNG 667.13 [identified as *L. mordax* by Thomas]), and samples from a nearby locality having similar habitat (Itabaiana, Sergipe)—whose external and skull morphology fit with those of the type series of *L. mordax* (ALP 8768–8770, 8812–8819)—we concluded that *L. mordax* has a light-brown ventral pelage, which is consistently darker than the paler ventral pelage of the type material of *L.*

dekeyseri and other samples of this species. The ventral pelage of specimens from Barra, Bahia (*L. inexpectata*) is similar to that of *L. dekeyseri*. Under "historical remarks" we discuss the reasons for previous assignments of pale-venter samples from the Caatinga of NE Brazil (= *L. inexpectata*) to *L. mordax*.

Lonchophylla inexpectata averages significantly smaller than *L. mordax* in all cranial dimensions except in POB and BCB (Table 1, Figure 4). This is particularly notable in the length of the mandible (MAL $\bar{x}$ = 15.6 mm, range [*R*] = 14.1–16.3 mm [*inexpectata*] versus $\bar{x}$ = 16.1 mm, *R* = 15.5–17.0 mm [*mordax*]). *L. inexpectata* can also be distinguished by the ventral pelage, which varies from whitish (e.g., USNM 238008, CM 99415) to pale greyish (near Avelaneous [e.g., CM 99432, 99437]), but near Buffy Brown in *L. mordax* (e.g., BM 1903.9.5.34, USNM 123392). The throat and the posterior region of the belly are consistently paler, tending to whitish, in *L. inexpectata* (Figure 5).

Lonchophylla inexpectata resembles *L. dekeyseri* in the pelage colour, but these species can be distinguished by qualitative and quantitative cranial characteristics. *Lonchophylla inexpectata* is significantly larger than *L. dekeyseri* in all length measurements of skull and rostrum (GLS, CIL, BAL, MTL, M1M3, MAL, MAN), but *L. dekeyseri* averages slightly larger in those measurements of the width of skull and rostrum (BAC, POB, BCB, MAB), indicating a longer but narrower skull in *L. inexpectata* (Table 1). *L. inexpectata* can be distinguished from *L. dekeyseri* by the narrower first upper premolar (P3) in occlusal view, with lingual lobe absent or obsolete (in contrast with the usually more robust P3, which has a small or moderately developed inner lobe in *dekeyseri* [Figure 6]); absence of a deep longitudinal groove in the posterior surface of the canine; narrower and uninflated rostrum, with more widely projecting lacrimals (wider and more inflated rostrum, and lacrimal region almost indistinguishable in *dekeyseri*); upper molars (M1 and M2) with low crowns in lateral view (molars with higher crowns in *dekeyseri*); parastyle of M1 projecting labially over the posterior labial margin of the last upper premolar (P4); mesostyle of M1 shorter; metastyle of M1 well developed (reduced or absent in *dekeyseri* [Figure 6]); parastyle of M2 well developed but slender (well developed and more rounded in *dekeyseri*); mesostyle of M2 shorter; metastyle of M2 distinct, moderate or well developed (reduced or absent in *dekeyseri*).

Multivariate analysis. To test the results obtained from the morphological analyses, we performed a discriminant function analysis including samples we confidently assigned to *L. dekeyseri* (three groups from the Cerrado of Mid-western Brazil), *L. inexpectata* (two groups from the Caatinga of NE Brazil), and *L. mordax* (one group from the Caatinga of NE Brazil, and one group from the Atlantic Forest–Caatinga ecotone in NE Brazil). The first two discriminant functions (DF1, DF2) summarized 47% and 40% of the total variation, respectively (Table 2). All samples grouped as expected, confirming the cohesive pattern retrieved from the morphological analysis. Centroids for samples assigned to *L. inexpectata* were distinct from those of *L. dekeyseri* and *L. mordax* across the first two axes, and only a few scores of *L. inexpectata* are within the dispersal cloud of *L. mordax* (Figure 7). The three species overlap partially across the first axis, but *L. inexpectata* distinguishes from *L. dekeyseri* and *L. mordax*

Figure 5. Ventral (above) and dorsal (below) pelage colours of L. mordax **A, B** (USNM 123392, paratype), and *L. inexpectata* **C, D** (CM 99432) **E, F** (CM 99416) **G, H** (CM 99415) **I, J** (USNM 238008, holotype).

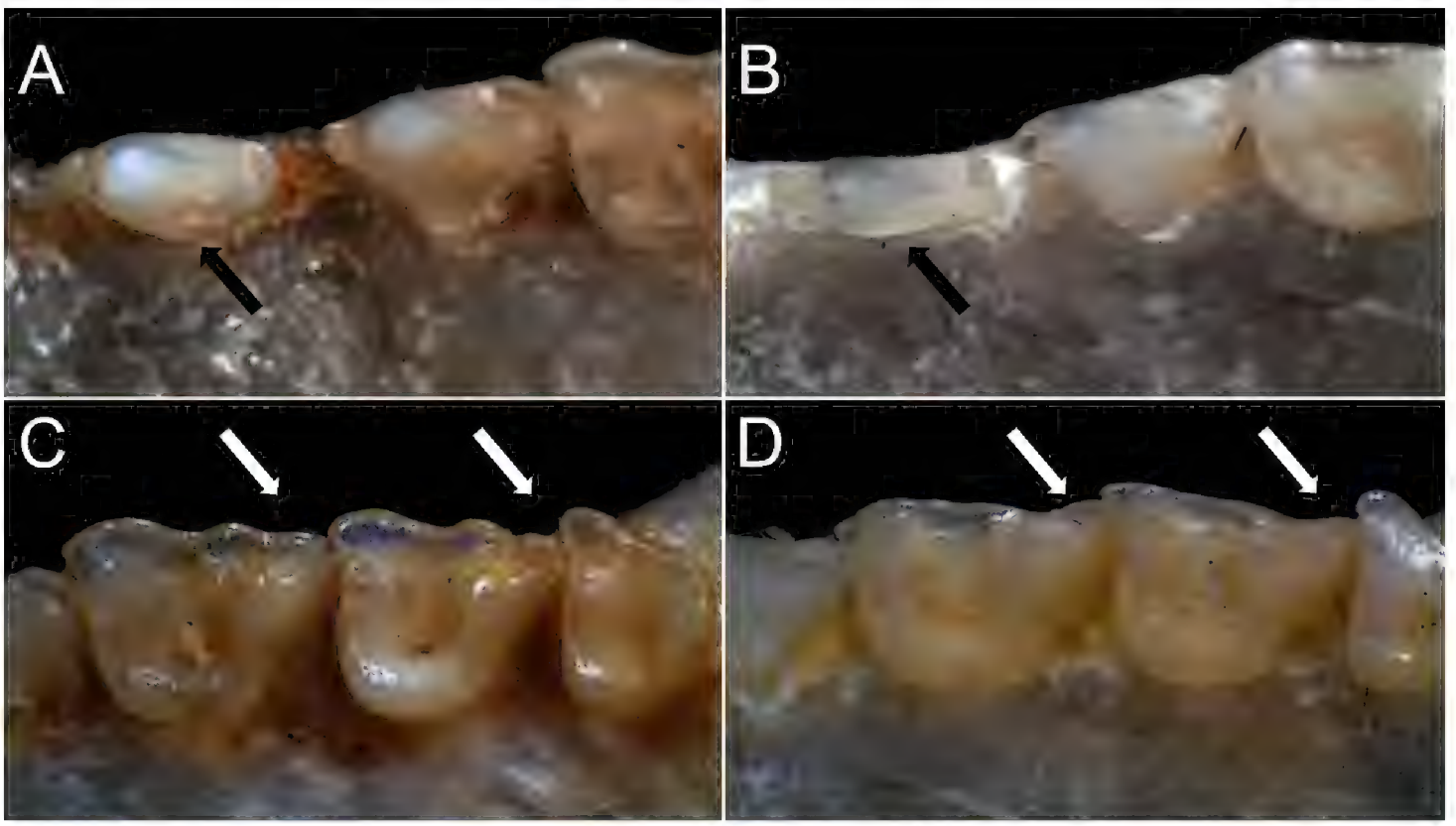

Figure 6. Upper dentition of *L. dekeyseri* **A, C** (LDM 3185) and *L. mordax* **B, D** (ALP 6149). **A, B** Moderate inner lobe in the first upper premolar (P3) of *L. dekeyseri* **A** contrasting with the lingual lobe of P3 absent or very reduced in *L. mordax* **B** (similar condition observed in *L. inexpectata*) **C, D** metastyles of M1 and M2 reduced or absent in *dekeyseri* **C** contrasting with the metastyles well developed and distinct in *L. inexpectata* and *L. mordax* **D**.

Table 2. Vector correlation coefficients (loadings) between original variables and discriminant functions (DF1, DF2) for samples of *L. dekeyseri*, *L. inexpectata* and *L. mordax*.

	DF1	**DF2**
Characters	46.5%	40.4%
GLS	0.724	0.021
CIL	0.706	-0.130
MAB	0.240	0.388
BCB	0.268	0.413
POB	-0.149	0.261
BAC	0.117	0.336
BAM	0.413	0.193
M1M3	0.226	0.477
MTL	0.523	0.151
MAL	0.645	0.100

along the second axis. Scores for *L. inexpectata* had very low positive to high negative values along the DF2, whereas those for *L. dekeyseri* and *L. mordax* have low negative to high positive values along this axis.

Etymology. The name "*inexpectata*" is Latin for "unexpected", in allusion to the unexpected (at least for the authors) new taxonomic status of pale-venter populations of *Lonchophylla* from the Caatinga of North-eastern Brazil.

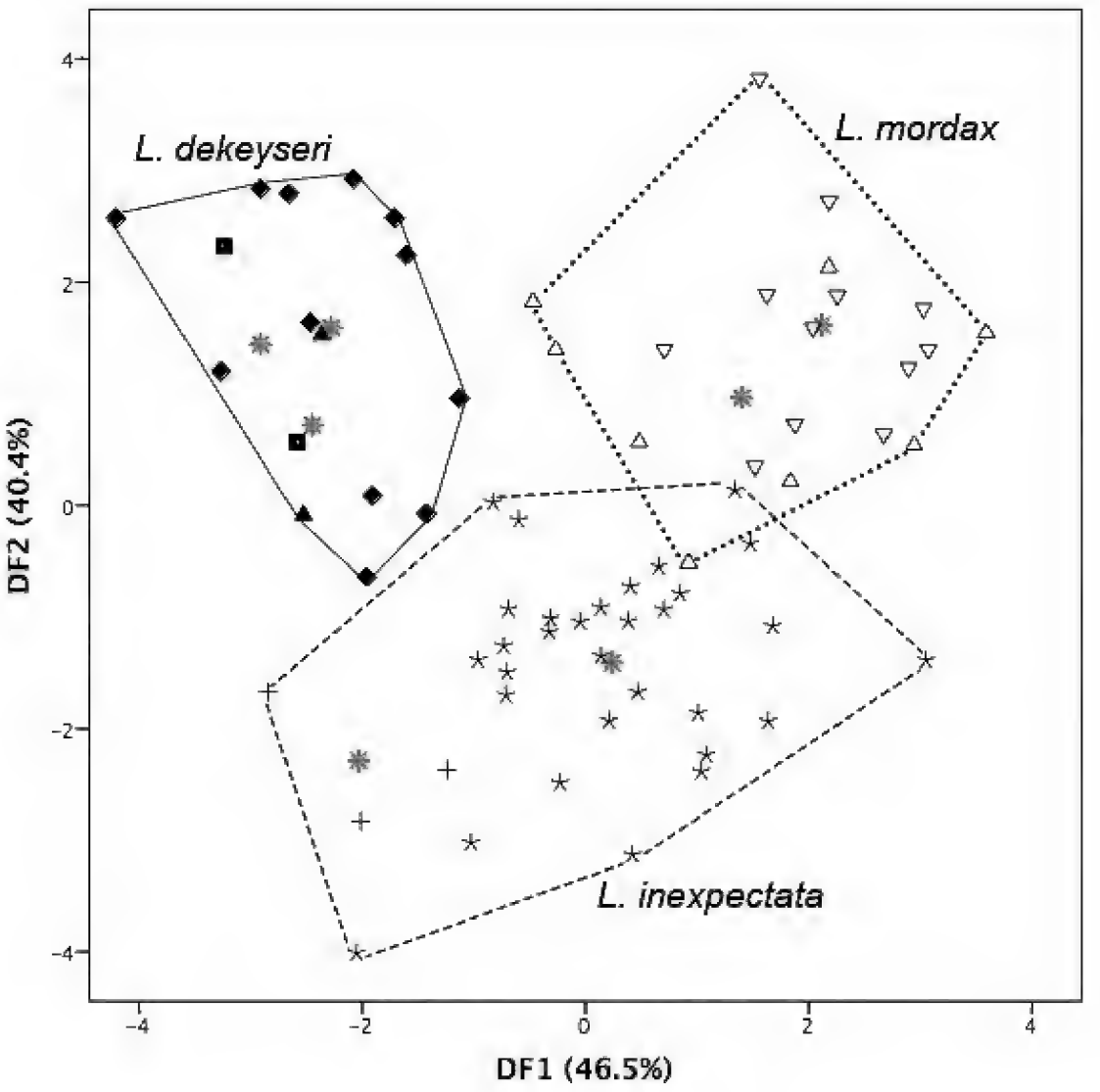

Figure 7. Plots of multivariate individual scores in the first two discriminant functions (DF1, DF2). Samples: *Lonchophylla dekeyseri* (Goiás [black diamonds, *N* = 12]; Mato Grosso do Sul [black squares, *N* = 2]; Distrito Federal [black triangles, *N* = 2]), *L. inexpectata* (Barra, Bahia [crosses, *N* = 3]; Exu, Pernambuco [stars, *N* = 31]), and *L. mordax* (Itabaiana, Sergipe [white triangles, *N* = 8]; Grota do Angico, Sergipe [white inverted triangles, *N* = 12]). Centroid groups are marked with grey asterisks.

Key to the Brazil's species of *Lonchophylla*

1 Proximal portion of the dorsal surface of the forearm covered with fur; upper canines distinctly grooved along the anterior surface; P4 narrow in occlusal view, with inner lobe reduced and lingual root displaced posteriorly..... **2**

– Proximal portion of the dorsal surface of the forearm not conspicuously furred; upper canines lacking a groove along the anterior surface; P4 robust, with inner lobe well developed and lingual root in the median portion of the tooth..... **3**

2 Smaller size; forearm length 37 mm or less; pale-brownish ventral fur; tip of the tragus rounded; parastyles, mesostyles and metastyles of M1 and M2 absent or poorly developed ..... ***Lonchophylla peracchii***

– Larger size; forearm length 39 mm or more; pale-greyish ventral fur; tip of the tragus pointed; parastyles, mesostyles and metastyles of M1 and M2 well developed..... ***Lonchophylla bokermanni***

3	P3 robust in occlusal view, with lingual lobe varying from small to moderately developed projection; presence of a conspicuous longitudinal groove along the posterior surface of the canine; metastyle of M1 and M2 absent or reduced ... ***Lonchophylla dekeyseri***
–	P3 narrow in occlusal view, usually without inner lobe or with a reduced lobe; absence of a conspicuous longitudinal groove along the posterior surface of the canine; metastyle of M1 and M2 distinct and developed..... **4**
4	Ventral fur pale-brownish; mandibular length 15.5–17.0 mm ..... ***Lonchophylla mordax***
–	Ventral fur whitish or pale-greyish on the throat and abdomen (particularly on the posterior region of the belly); mandibular length 14.1–16.3 mm ..... ***Lonchophylla inexpectata***

Discussion

Historical remarks. Previous assignments of *L. inexpectata* to *L. mordax* seem to have originated with Lima (1926: 36) who based his account of *L. mordax* on the series from Barra, which was collected by Garbe and deposited in the Museu de Zoologia da Universidade de São Paulo. Barra is in the *sertão* of Bahia (Caatinga), ca. 450–500 km west of Lamarão, which is in the *agreste* of Bahia (transition between Atlantic Forest and Caatinga; type locality of *L. mordax*). Thomas (1903: 459) described *L. mordax* as follows:

> *General external appearance, so far as can be judged by skins, exactly as in* Glossophaga soricina, *except that the colour averages paler. The type is near "cinnamon-brown" above, the bases of the hairs whitish, and "wood-brown" below, but there is some variation in tone, and the darker specimens are quite as dark as the paler examples of* Glossophaga *obtained at the same place.*

Lima (1926) seems to have misinterpreted Thomas (1903) where he reported that "darker specimens [of *L. mordax*] are quite as dark as the paler examples of *Glossophaga* obtained at the same place." Lima's conclusion might be biased by the series he had at hand, primarily composed by pale-venter specimens from Barra, Bahia. However, at that time, *L. mordax* was unquestionably the closest species—geographically and morphologically. Although Lima had identified this series from Barra as *L. mordax*, the label of the USNM 238008 bears the notation "*Subsp. n. ?*"

Vieira (1942: 321) followed Lima (1926) and based his account of *L. mordax* on the same specimens collected by Garbe. Both recognized *L. mordax* as a pale-venter species. This was followed by Taddei et al. (1983) who compared the species they were describing (*L. dekeyseri*) with "*L. mordax*"—the other pale-venter species from NE Brazil, according to those authors. However, according to Thomas (1903), the ventral pelage of *L. mordax* is "wood-brown", but with some variation, with darker specimens almost as dark as paler specimens of *Glossophaga* from the same area. *Glossophaga*

soricina (Phyllostomidae)—the only species of the genus that occur in the region—has ventral pelage varying from "buffy to fuscous" (Alvarez et al. 1991).

Taxonomic remarks. Molecular and morphological analyses have recovered *Lonchophylla* (sensu Griffiths and Gardner 2008) as a paraphyletic assemblage (Dávalos and Jansa 2004, Woodman and Timm 2006, Woodman 2007). Combining evidence from nuclear and mitochondrial genes, karyotypes and skull morphology, Parlos et al. (2014) also retrieved *Lonchophylla* as paraphyletic. Based on their findings, Parlos et al. (2014) described *Hsunycteris* and moved three species into this new genus—*thomasi* J. A. Allen, 1904; *cadenai* Woodman & Timm, 2006; and *pattoni* Woodman & Timm, 2006. As a result, *Lonchophylla* comprised 12 South and Central American species (Parlos et al. 2014). However, several species were not assessed, including *L. mordax*—the type species of *Lonchophylla*. According to Parlos et al. (2014), the two genera can be distinguished by size (with species in *Lonchophylla* larger than those in *Hsunycteris*), qualitative cranial features, and karyotypes (*Lonchophylla* spp.: diploid number [2n] = 48, fundamental autosomal number [NF] = 50; *Hsunycteris* spp.: 2n = 30–36, NF = 34–50).

The samples we have available show that *L. dekeyseri* and *L. mordax* are in parapatry with *L. inexpectata*: *L. dekeyseri* occurs in the Cerrado of Brazil and possibly in the Bolivian savannah (USNM 584472, 584473) and the Cerrado–Caatinga ecotone in NE Brazil (DZSJRP 11459); and *L. mordax* occurs in the Atlantic Forest–Caatinga ecotone (*agreste*), and along the eastern border of the Caatinga (*sertão*). We are not convinced that *L. dekeyseri* occurs in the Bolivian savannah and in the Cerrado–Caatinga ecotone in NE Brazil. One of the specimens supporting these records was examined a long time ago (DZSJRP 11459), and the other two (USNM 584472, 584473) are distinct from other samples of *L. dekeyseri* as determined in a previous discriminant function analysis. These specimens are not included in this analysis because we were not able to compare them with samples from other localities. Records previously assigned to *L. mordax* from N Brazil are based primarily on Handley (1967) and Piccinini (1974), and those identifications were not confirmed in subsequent surveys. We speculate that they are misidentifications of *L. thomasi*, now *Hsunycteris thomasi*. Similarly, previous unvouchered records of *L. mordax* from the Atlantic Forest of SE Brazil apparently represent *L. peracchii* based on the identity of material we have examined from nearby localities.

After Parlos et al.'s (2014) assignment of *L. thomasi* J. A. Allen, 1904 to *Hsunycteris*, *L. inexpectata* is the fifth *Lonchophylla* reported from Brazil—all pending phylogenetic positioning. There are several specimens pending verification of identity, particularly those from the Caatinga. Additional material, particularly from NE and Mid-western Brazil, will be important to a clearer understanding of the taxonomic diversity, and the geographic distribution of Brazilian species of *Lonchophylla*.

Acknowledgements

We thank the following curators and collections staff for loans, information on specimens in their care, for making collections available, or for assistance during museum work:

A. L. Peracchi (UFRRJ, Brazil), E. Morielle-Versute (UNESP, Brazil), J. A. de Oliveira (MN, Brazil), J. Wible, S. McLaren (CM, USA), K. Helgen, D. Lunde (NMNH, USA), M. Ruedi (MHNG, Switzerland), N. Simmons, E. Westwig (AMNH, USA), M. Nascimento, and Y. L. R. Leite (UFES, Brazil). R. Portela Miguez (BMNH, England) provided images of the holotype of *L. mordax*. M. R. Nogueira (UENF, Brazil) provided access to material he collected and assisted us in the morphological analyses. C. Aires (UMC), D. Seripierri, and F. Nascimento (MZUSP) helped us with literature about E. Garbe. A. L. Gardner (USGS Patuxent Wildlife Research Center, USA) revised a previous draft of the manuscript. This work was supported by the Brazilian National Council for Scientific and Technological Development / Science Without Borders Program (CNPq 202612/2012), and the Smithsonian Institution.

References

Albuja VL, Gardner AL (2005) A new species of *Lonchophylla* Thomas (Chiroptera: Phyllostomidae) from Ecuador. Proceedings of the Biological Society of Washington 118: 442–449. doi: 10.2988/0006-324X(2005)118[442:ANSOLT]2.0.CO;2

Allen JA (1904) New bats from tropical America, with note on species of *Otopterus*. Bulletin of the American Museum of Natural History 20: 227–237.

Alvarez J, Willig MR, Jones JK, Webster WD (1991) *Glossophaga soricina*. Mammalian Species 379: 1–4. doi: 10.2307/3504146

Astúa D, Guerra DQ (2008) Caatinga bats in the mammal collection of the Universidade Federal de Pernambuco. Chiroptera Neotropical 14: 326–338.

Dávalos LM, Jansa SA (2004) Phylogeny of the Lonchophyllini (Chiroptera: Phyllostomidae). Journal of Mammalogy 85: 404–413. doi: 10.1644/1545-1542(2004)085<0404:POTLCP>2.0.CO;2

Dias D, Peracchi AL, Silva SSP (2002) Quirópteros do Parque Estadual da Pedra Branca, Rio de Janeiro, Brasil (Mammalia, Chiroptera). Revista Brasileira de Zoologia 19 (Supl. 2): 113–140. doi: 10.1590/S0101-81752002000600012

Dias D, Esbérard CEL, Moratelli R (2013) A new species of *Lonchophylla* (Chiroptera, Phyllostomidae) from the Atlantic Forest of southeastern Brazil, with comments on *L. bokermanni*. Zootaxa 3722(3): 347–360. doi: 10.11646/zootaxa.3722.3.4

Esbérard CEL (2003) Diversidade de morcegos em área de Mata Atlântica regenerada no sudeste do Brasil. Revista Brasileira de Zoociências 5:189–204.

Esbérard CEL, Jordão-Nogueira T, Luz JL, Melo GGS, Mangolin R, Jucá N, Raíces DSL, Enrici MC, Bergallo HG (2006) Morcegos da Ilha Grande, Angra dos Reis, RJ, Sudeste do Brasil. Revista Brasileira de Zoociências 8: 147–153.

Gardner AL (2008) Mammals of South America, vol. 1, marsupials, xenarthrans, shrews, and bats. University of Chicago Press, Chicago. [Dated 2007, published 31 March, 2008]

Griffiths TA, Gardner AL (2008) Subfamily Lonchophyllinae. In: Gardner AL (Ed.) Mammals of South America, vol. 1, marsupials, xenarthrans, shrews, and bats. University of Chicago Press, Chicago, 244–255. [Dated 2007, Published 31 March, 2008]

Handley Jr. CO (1966) Checklist of the mammals of Panama. In: Wenzel RL, Tipton VJ (Eds) Ectoparasites of Panama. Field Museum of Natural History, Chicago, 753–795.

Handley Jr. CO (1967) Bats of the canopy of an Amazonian Forest. Atas do Simpósio sôbre a Biota Amazônia 5: 211–215.

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 1–9.

Koopman KF (1981) The distributional patterns of New World nectar-feeding bats. Annals of the Missouri Botanical Garden 68: 352–69. doi: 10.2307/2398802

Lima JL (1926) Os morcegos da collecção do Museu Paulista. Revista do Museu Paulista, 43–127.

Mares MA, Willig MR, Streilein KE, Lacher Jr. TE (1981) The mammals of northeastern Brazil: a preliminary assessment. Annals of Carnegie Museum 50: 81–137.

Nogueira MR, Dias D, Peracchi AL (2007) Subfamília Glossophaginae. In: dos Reis NR, Peracchi AL, Pedro WA, Lima IP (Eds) Morcegos do Brasil. Privately published, Londrina, 45–59.

Parlos JA, Timm RM, Swier VJ, Zeballos H, Baker R (2014) Evaluation of paraphyletic assemblages within Lonchophyllinae, with description of a new tribe and genus. Occasional Papers, Museum of Texas Tech University 320: 1–23.

Pedro WA, Passos FC (1995) Occurrence and food habits of some bat species from the Linhares Forest Reserve, Espírito Santo, Brazil. Bat Research News 36: 1–2.

Peracchi AL, Lima IP, Reis NR, Nogueira MR, Ortencio-Filho H (2011) Ordem Chiroptera. In: dos Reis NR, Peracchi AL, Pedro WA, Lima IP (Eds) Mamíferos do Brasil, second edition, Editora da Universidade Estadual de Londrina, Londrina, 155–234.

Pereira-Barreto M, Siqueira AF, Ferriolli-Filho F, Carvalheiro JR, Albuquerque RDR, Funayama GK (1968) Estudos sôbre reservatórios e vectores silvestres do "Trypanosoma cruzi". XXVII: infecção natural de quirópteros pelo "Trypanosoma vespertilionis" Bataglia, 1904. Revista Brasileira de Biologia 28: 147–155.

Phillips CJ (1971) The dentition of Glossophaginae bats: development, morphological characteristics, variation, pathology, and evolution. Miscellaneous Publications, Museum of Natural History, University of Kansas 54: 1–138.

Piccinini RS (1974) Lista provisória dos quirópteros da coleção do Museu Paraense Emílio Goeldi (Chiroptera). Boletim do Museu Paraense Emílio Goeldi 77: 1–32.

Prado D (2003) As caatingas da América do Sul. In: Leal IR, Tabarelli M, Silva JMC (Eds) Ecologia e conservação da Caatinga. Universidade Federal de Pernambuco, Recife, 3–73.

Sazima I, Vizotto LD, Taddei VA (1978) Uma nova espécie de *Lonchophylla* da Serra do Cipó, Minas Gerais, Brasil (Mammalia, Chiroptera, Phyllostomidae). Revista Brasileira de Biologia 38: 81–89.

Taddei VA, Vizotto LD, Sazima I (1978) Notas sobre *Lionycteris* e *Lonchophylla* nas coleções do Museu Paraense Emílio Goeldi (Mammalia, Chiroptera, Phyllostomidae). Boletim do Museu Paraense Emílio Goeldi, Série Zoologia 92: 1–14.

Taddei VA, Vizotto LD, Sazima I (1983) Uma nova espécie de *Lonchophylla* do Brasil e chave para identificação das espécies do gênero (Chiroptera, Phyllostomidae). Ciência e Cultura 35: 625–629.

Thomas O (1903) Notes on South-American monkeys, bats, carnivores, and rodents, with descriptions of new species. Annals and Magazine of Natural History series 7, 12: 455–464. doi: 10.1080/00222930308678880

Vieira COC (1942) Ensaio monográfico sobre os quirópteros do Brasil. Arquivos de Zoologia do Estado de São Paulo 3(8): 219–471.

Vieira COC (1955) Lista remissiva dos mamíferos do Brasil. Arquivos de Zoologia do Estado de São Paulo 8(11): 341–474.

Voss RS, Lim BK, Díaz-Nieto JF, Jansa SA (2013) A new species of *Marmosops* (Marsupialia: Didelphidae) from the pakaraima highlands of Guyana, with remarks on the origin of the endemic Pantepui mammal fauna. American Museum Novitates 3778: 1–27.

Willig MR (1983) Composition, microgeographic variation, and sexual dimorphism in Caatingas and Cerrado bat communities from northeast Brazil. Bulletin of Carnegie Museum of Natural History 23:1–131.

Woodman N (2007) A new species of nectar-feeding bat, genus *Lonchophylla*, from western Colombia and western Ecuador (Mammalia: Chiroptera: Phyllostomidae). Proceedings of the Biological Society of Washington 120: 340–358. doi: 10.2988/0006-324X(2007)120[340:ANSONB]2.0.CO;2

Woodman N, Timm RM (2006) Characters and phylogenetic relationships of nectar-feeding bats, with descriptions of new *Lonchophylla* from western South America (Mammalia: Chiroptera: Phyllostomidae: Lonchophyllini). Proceedings of the Biological Society of Washington 119: 437–476. doi: 10.2988/0006-324X(2006)119[437:CAPRON]2.0.CO;2

Appendix

Specimens examined. Abbreviations for collections are in "Methods".

Lonchophylla bokermanni (08): Brazil, Minas Gerais: Diamantina (18°23'S, 43°61'W: MN 79996, MN 79997); Serra do Cipó (19°16'S, 43°36'W: DZSJRP 10342 [paratype], 10347 [holotype], 10408 [paratype], 11410 [paratype], 11411 [paratype], 10412 [paratype; referred in the original description as ZUEC 585]).

Lonchophylla dekeyseri (16): Brazil, Distrito Federal: Parque Nacional de Brasília (15°41'S, 47°59'W: DZSJRP 10099 [holotype]); unknown locality (ALP 6706, 6707). Brazil, Goiás: Mambaí (14°29'S, 46°06'W: LDM 283, 3008, 3065, 3066, 3104, 3169, 3170, 3184, 3185, 3201, 3215, 3270). Brazil, Mato Grosso do Sul: Corumbá (19°61'S, 57°45'W: LDM 2642).

Lonchophylla cf. *dekeyseri* (3): Bolivia, Santa Cruz: Velasco (13°54'27"S, 60°48'52.92"W: USNM 584472, 584473). Brazil, Piauí: Sete Cidades, Piracuruca (03°56'S, 41°44'W: DZSJRP 11459 [paratype of *dekeyseri*]).

Lonchophylla inexpectata: Brazil, Bahia (43): Barra (12°42'S, 41°33'W: USNM 238008 [holotype], AMNH 235608, FMNH 21077, 21078 [paratypes]). Brazil, Pernambuco: Buíque, Serra do Catimbau (08°37'S, 37°09'W: FMNH 137414 [paratype]); 17 km south of Exu (07°41'S, 39°32'W: CM 99413–99450).

Lonchophylla cf. *inexpectata* (1): Brazil, Bahia: Andaraí, unknown locality (ALP 3686).
Lonchophylla mordax (35): Brazil, Bahia: Lamarão (11°45'S, 38°55'W: BM 1903.9.5.34 [holotype], USNM 123392 [paratype]). Brazil, Sergipe: Itabaiana (10°68'S, 37°42'W: ALP 6149, 8769, 8770, 8812–8819); Parque Nacional Grota do Angico (09°65'S, 37°67'W: ALP 9747, 9752, 9755, 9757, 9759, 9761, 9762, 9768, 9769, 10075–10082, 10084–10088).
Lonchophylla peracchii (75): Brazil, Espírito Santo: Sooretama, BR-101, Km 105, Reserva Biológica de Sooretama (19°1'48.97"S, 40°1'8.976" W: UFES 2046, 2047, 2117) Brazil, Rio de Janeiro: Angra dos Reis, Ilha da Gipóia (23°02'S, 44°21'W: LDM 4200, 4423); Angra dos Reis, Ilha Grande (23°10'S, 44°12'W: DZSJRP 15159 [paratype], 15160, 15161, 15162 [holotype], 15163 [paratype], LDM 246, 2090, 3450, 3896, 3897, 4052, 4233, 4533); Cambuci (21°34'S, 41°54'W: LDM 4250, 4253, 4477); Casimiro de Abreu, Morro de São João (22°29'S, 41°58'W: LDM 2219, 2245, 4113, 4222, 4226, 4227); Itaguaí, Ilha de Itacuruçá (23°56'S, 43°53'W: LDM 5085); Mangaratiba, Vale do Rio Sahy (23°55'S, 43°59'W: LDM 5128); Nova Iguaçú, Reserva Biológica do Tinguá (22°39'S, 43°34'W: ALP 6265, 6560, 6561, 6283, 6284, 6556, 6656–6559); Parati (23°19'S, 44°38'W: LDM 996, 997); Rio de Janeiro, Estrada Rio-Santos (23°55'S, 43°16'W: LDM 5008, 5010); Rio de Janeiro, Floresta da Tijuca (22°57'S, 43°24'W: LDM 1064, 1460); Rio de Janeiro, Jardim Botânico (22°58'S, 43°13'W: LDM 875); Rio de Janeiro, Parque Estadual da Pedra Branca (22°52'S, 43°23'W: ALP 5664, 5820, 5860); Rio de Janeiro, Reserva do Grajaú (22°55'S, 43°16'W: ALP 1783–1785, LDM 237, 238, 246–248, 250, 270, 280, 281, 345, 395, 531–533, 1359, 1495–1497, 1499); Rio de Janeiro, Reserva Rio das Pedras (22°59'S, 44°06'W: LDM 1781, 3700); Teresópolis, Parque Nacional da Serra dos Órgãos (22°26'S, 42°59'W: ALP 6482). Brazil, São Paulo: Ubatuba, Picinguaba (23°18'S, 44°53'W: ALP 10242).

Supplementary material 1

Occurrence localities for Bolivian and Brazilian species of *Lonchophylla*
Authors: Ricardo Moratelli, Daniela Dias
Data type: Occurrence localities
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.